

**A REASSESSMENT OF REPTILIAN DIVERSITY ACROSS
THE CRETACEOUS-TERTIARY BOUNDARY**

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A REASSESSMENT OF REPTILIAN DIVERSITY ACROSS THE CRETACEOUS–TERTIARY BOUNDARY

Robert M. Sullivan¹

ABSTRACT. A global species level account for marine, flying, and terrestrial reptilian families as well as the documentation of their biostratigraphic occurrence in Late Cretaceous (late Senonian) through early Paleogene (Eocene) strata unequivocally demonstrates a gradual extinction pattern of reptilian species through the Cretaceous–Tertiary transition and is inconsistent with arguments to the contrary in support of an isochronous catastrophic mass extinction event. The apparent evidence for a supposed mass extinction of many of

the Cretaceous reptiles has been created by the use of higher taxonomic categories (principally families) and unnatural assemblages of out-group categories (paraphyletic groups) coupled with poorly resolved biostratigraphic data. A reassessment of the reptilian species lineages that approach or transgress the Cretaceous–Tertiary boundary clearly demonstrates that there was no mass extinction of dinosaurs and other reptiles at the termination of the Cretaceous Period.

Evolutionary biologists are agreed that the species is the only taxon with objective reality and it is at this level that both evolution and extinction takes place.

Norman Newell, 1982:260

INTRODUCTION

Asteroid impact, comet encounter, and supernova explosion have all been postulated as primary causes for the supposed global mass extinctions in the Late Cretaceous (Russell and Tucker, 1971; L. Alvarez et al., 1980; W. Alvarez et al., 1982, 1984a; L. Alvarez, 1983; W. Alvarez et al., 1984b). Volcanism, nemesis event, and global wildfires have been recently proposed by various individuals (Bailey, 1984; Hut, 1984; Raup and Sepkoski, 1984; Torbett and Smoluchowski, 1984; Gledhill, 1985; Officer and Drake, 1985; Wolbach et al., 1985). This Late Cretaceous mass extinction has been viewed by many workers to be an isochronous phenomenon, affecting both marine and terrestrial realms. It is, however, the terrestrial component of the Late Cretaceous fauna (largely dominated by the dinosaurs), that receives the most attention with regard to this mass extinction. The occurrence and nature of the “Late Cretaceous mass extinction” has led to debates within the scientific community (Russell, 1977, 1979, 1982b, 1982c, 1982d; Clemens et al., 1981; Archibald and Clemens, 1982a, 1982b; Asaro et al., 1982; Clemens, 1982; and others). However, the conspicuous disappearance of the archaic dinosaurs along with the marine and flying reptiles often cited as evidence for a mass extinction event at the end

of the Cretaceous, is in fact, an illusion, created by scenarios based upon misinterpreted biostratigraphic data and antiquated taxonomic practices.

The gradualistic nature of the Cretaceous–Tertiary faunal change has been documented by many recent works. Among the more important are Archibald (1981) for mammals, Kauffman (1982) for marine invertebrates, Tappan (1982) for faunas and floras of the Phanerozoic, and Sloan (1976), Van Valen and Sloan (1977), Schopf (1982), and Sloan et al. (1986) for Late Cretaceous dinosaurs. Other recent studies, such as the sedimentary facies study of the classic Late Cretaceous terrestrial sequence at Bug Creek, Montana, by Fastovsky and Dott (1986), neither support nor refute either gradualistic or catastrophic models for the end of the Cretaceous while that of Signor and Lipps (1982) suggested that the gradualistic decline in taxa at the end of the Cretaceous reflects inadequate sampling. However, contrary to these and

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other investigations, there are an adequate amount of stratigraphic and taxonomic data to suggest a non-catastrophic turnover of Late Cretaceous species. Despite this fact, most paleontologists have been very slow to present these data in a convincing way and many paleontologists still believe that a mass extinction took place at the end of the Cretaceous Period.

Dale Russell (hereafter Russell) has long been an advocate of the Late Cretaceous dinosaurian mass extinction as witnessed by his many publications (Russell and Tucker, 1971; Russell, 1975, 1977, 1979, 1982a, 1982b, 1982c, 1982d, 1984). Three of his papers (Russell, 1975, 1982d, 1984), which form the focus of this paper, have been particularly important in assessing the diversity of reptilian taxa near the Cretaceous–Tertiary (K–T) boundary and have supported the scenario of a catastrophic mass extinction for the dinosaurs.

Russell (1975, 1982d) presented diagrams illustrating the chronostratigraphic ranges of the reptilian families near the K–T boundary. Unfortunately, his diagrams in both instances neither accurately present the known chronostratigraphic ranges of the reptilian families in the detail necessary to demonstrate an isochronous event, nor do they accurately reflect true reptilian diversity through Late Cretaceous time. Other objections to his techniques have been adequately stated by Clemens et al. (1981) and Schopf (1982) and do not need to be repeated.

There are, however, some additional aspects of Russell's studies that do need to be addressed. Russell (1982d), in support of a mass extinction event for dinosaurs, has pointed to the large number of specimens found in *Late Cretaceous* strata, and not by the number of species known. As with his earlier study (Russell, 1975), many of these specimens (and taxa) had not been correlated with precision to late Maastrichtian strata. Russell's usage of "Upper Cretaceous" is misleading because there is an inherent danger that many of the higher taxonomic categories may be interpreted as being unequivocally late Maastrichtian in age, when in fact they may be older (late Santonian–middle Maastrichtian). Russell's (1982d) argument for numerous dinosaurs living at the time of the Cretaceous–Tertiary transition, based solely on the number of specimens known, *not* on the number of species, is irrelevant when assessing taxonomic diversity.

Taxonomic diversity can only be recognized by the number of clades at the species level, rather than the number of higher taxonomic categories. Family rankings do not in themselves reflect diversity, nor are they equivalent in rank or degree across groups. The extinction of families can only be viewed in terms of the last surviving species; the majority of species within a given family do not become extinct at the same time under normal circumstances. The use of higher taxonomic categories, such as families, in discussions of mass extinction without addressing species diversity through time, only continues to provide poorly resolved data (Valentine, 1974). Lack of agreement concerning the number and make-up of reptilian, particularly dinosaurian families, makes estimates of diversity based upon these and other higher taxonomic categories unreliable and does not provide any

information regarding species diversity, as Valentine (1974), Archibald and Clemens (1982b), Newell (1982), Raup (1982), and Sepkoski (1982) have recognized. To complicate matters, a number of the established dinosaurian families are now known to be non-monophyletic, and thus are unnatural groups. Continued employment of these taxonomic groupings in discussions of taxonomic diversity only serves to bias conclusions regarding extinction. Mass extinctions are thus, in large part, products of the utilization of higher taxonomic categories and use of out-group (paraphyletic) extinctions.

More recently, Russell (1984) attempted to present North American dinosaurian diversity for the entire Mesozoic based on the numbers of families and genera. This study is biased, not only because of the utilization of higher taxonomic categories as just outlined for his previous studies, but because it was largely provincial in scope, in that he failed to recognize land continuity between continents for much of the Mesozoic and the significance of the incomplete fossil record on the different continental masses, as well as the absence of certain dinosaurian families at the continental level. In addition, he failed to address the validity and/or the polyphyletic nature of many of the dinosaurian families discussed.

The purpose of this paper is to reassess the data for reptilian diversity across the K–T boundary. This reassessment is largely twofold. First, I will address the taxonomic diversity of Late Cretaceous (late Senonian) reptiles (based upon valid species in the fossil record) rather than simply relying on duration and extinction of higher taxonomic categories, such as families. Second, I will document, where necessary, the highest stratigraphic *in situ* occurrences of each taxon, as far as it can be assessed, and will treat this as the last occurrence. I will attempt to list all the valid late Senonian reptilian taxa (Santonian–Maastrichtian). However, any omission of a species or taxon, may be the result of either a) synonymy; b) not having been recognized by me as being valid (e.g., *nomen dubium*); or c) an oversight on my part. To this end, I hope that this study will provide a more accurate assessment of reptilian taxa and their biostratigraphic position than has been previously suggested by Russell (1975, 1982d, 1984).

For comparative purposes only, I present the durations of valid reptilian taxa in Table 1 so that comparisons can be made with the diagrams of Russell (1975, 1982d). It should be noted that the durations of dinosaurian families say nothing regarding the taxonomic diversity, nor does my chart indicate change in relative abundance of species through time. The number of reptilian species within a particular taxon is discussed in detail below. A few of the previously recognized dinosaurian and other reptilian families are monotypic and are treated at the species level. As Gauthier (1986) correctly pointed out, higher taxonomic categories established for one species are redundant and offer no additional information. Polyphyletic families are indicated by shutter quotes because they represent unnatural groupings. Other families, which are no longer considered valid, are also indicated by shutter quotes and are clearly identified. Taxa known solely from teeth (hereafter "tooth taxon" or "tooth taxa") are for the most part invalid, because phylogenetic relationships cannot

always be assessed. While it is apparent that a few families do become extinct near or at the K–T boundary based on the extinction of a last surviving taxon, many families appear

to drop out before, while others continue on through (Table 1).

BIOSTRATIGRAPHY AND AGE CORRELATIONS

Of paramount importance when considering Late Cretaceous reptilian diversity, in addition to taxonomic considerations just discussed, is the documentation of precise stratigraphic horizon(s) in which individual species are known to occur. There has been little agreement among paleontologists and biostratigraphers as to the correlation of many Late Cretaceous and Tertiary stratigraphic units, at both an intra- and intercontinental level, owing to the lack of intertonguing terrestrial/marine rocks and lack of global index fossils. It is, however, necessary to correlate Late Cretaceous terrestrial sequences to the Late Cretaceous marine standard, so that accurate relative age dating can be achieved. Many workers have suggested correlations for Late Cretaceous terrestrial “dinosaur-bearing” sediments to the marine standard; among the more important contributions are those of L. Russell (1964, 1975), Russell and Chamney (1967), Kielan-Jaworowska (1974), Gradziński et al. (1977), Fox (1978), Russell and Singh (1978), Lerbekmo et al. (1979a, 1979b), Russell (1979, 1982a, 1982c, 1982d), Karczewska and Ziembinska-Tworzydło (1983), Lillegraven and McKenna (1986), Fassett (1987), Fassett et al. (1987), Lucas et al. (1987), and Newman (1987). All of these workers present differing correlations, born of conflicting data.

Not only is accurate correlation between Late Cretaceous marine and terrestrial units necessary to recognize precise relative ages for these strata that involve a K–T boundary “mass extinction” event, but the recognition and correlation of the K–T boundary is desirable also. However, because different criteria have been used in the definition of the K–T boundary (iridium anomaly, pollen changes, foraminifera, and the highest stratigraphic occurrence of the last “dinosaur”), and because these criteria have not been conclusively demonstrated to be isochronous, discussions of mass extinction are often circular in reasoning. Stratigraphers and paleontologists have yet to reach a consensus as to what criterion defines the Cretaceous–Tertiary boundary. Berry’s (1984) suggestion to use the distinctive clay (iridium anomaly) as the standard K–T boundary because it marks “one of the most abrupt set of extinctions among both marine and terrestrial organisms in the record of life” (Berry, 1984:152) is seriously flawed because it is not supported by either taxonomic or biostratigraphic evidence.

The diachronous nature of the K–T boundary seems almost certain. This fact has been illustrated by Fassett (1982) in the San Juan Basin, where dinosaur remains lie above the K–T boundary as defined by the pollen “spike,” which is supposedly coincident with the iridium anomaly that defines the K–T boundary for some workers. A similar situation is

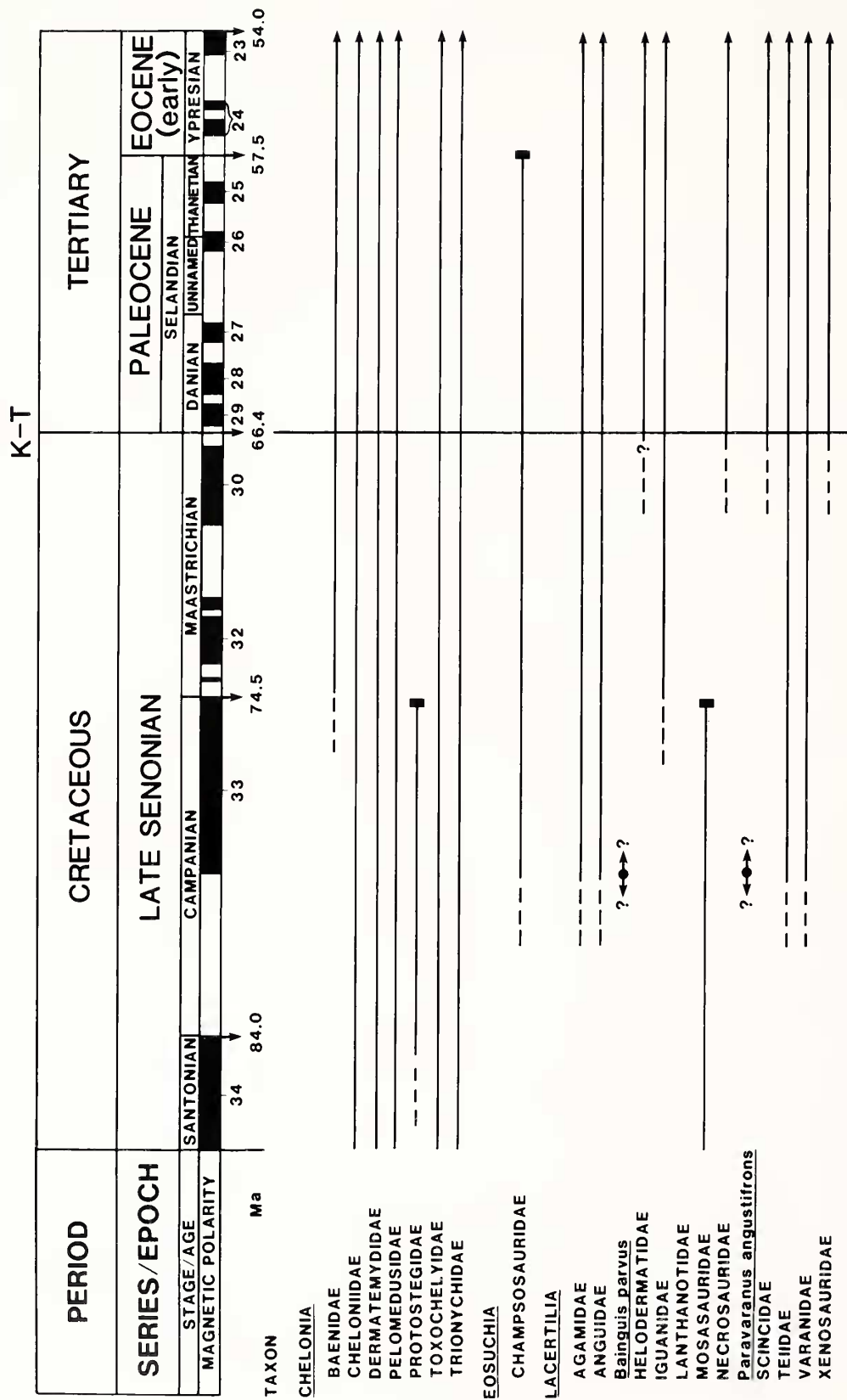
currently being studied in the Bug Creek area of Montana by Sloan et al. (1986). Accepting the iridium anomaly as the K–T boundary, their interpretation of the stratigraphic sequence and the occurrence of dinosaur fossils suggest that the supposed asteroid impact occurred well before the mass extinction event, and that dinosaurs gradually became extinct during the Paleocene. These studies demonstrate the diachronous nature of the K–T boundary owing to different sets of criteria.

For this paper, I am not particularly concerned about where one draws the K–T boundary, as it is largely irrelevant for present purposes. Biostratigraphic data for taxa discussed below are derived from many sources (Table 2), some from the original workers as well as from correlations provided by McGookey et al. (1972) and Fox (1978) which are viewed as the most consistent and middle-of-the-road, compared to the more radical correlations presented by Karczewska and Ziembinska-Tworzydło (1983) and Lillegraven and McKenna (1986). Absolute dates for the Late Cretaceous marine stages and the Tertiary are continually being refined. Kent and Gradstein (1985) and Berggren et al. (1985) have revised Harland et al.’s (1982) geochronology for the Jurassic, Cretaceous, and Cenozoic, respectively, which is accepted here.

In an attempt to reduce the repetitiveness in citing marine ages for the more common formations or principal dinosaur-bearing units, the reader is referred to Table 2 for the marine standard correlatives and magnetic polarity zones.

It is common knowledge that the fossil record is not complete and that vertebrate faunas are not continuous throughout the entire vertical extent of a particular formation (e.g., Hell Creek, Lance, Nacimiento formations, etc.) but typically occur as restricted fossil-bearing horizons, or intervals, within strata. Terms, such as “Lancian,” can only be applied to the fauna and not to strata in which the fauna occurs. Unfortunately, these terms are often misused, and are applied to unfossiliferous strata above and below the characteristic fauna (e.g., see examples in Lillegraven and McKenna, 1986: 41, table 10). The relative age of these barren intervals cannot be determined with any level of confidence. Because of this fact, I choose to abandon the age concept North American Land Mammal “ages” (“NALMAs”) in my chart (Table 1), a convention that has been employed by most North American vertebrate paleontologists, that supposedly covers all of Cenozoic and now Late Cretaceous time (Wood et al., 1941; Savage, 1962; Tedford, 1970; Lillegraven and McKenna, 1986). North American Land Mammal “ages” as they are currently used, do not provide any greater time resolution than do formally recognized standard ages.

Table 1. Range chart for reptilian families and other taxa spanning the Cretaceous-Tertiary boundary (exclusive of birds). Traditional dinosaurian taxa that become extinct at the boundary are typically represented by only one or two species. Thus a major reduction in species diversity occurred prior to the end of the Cretaceous. Species diversity is not indicated by the diagram (see text for discussion). Shutter quotes around taxon indicates polyphyly.



SERPENTES

ANILIIDAE

BOIDAE

Dinilysia patagonia

CROCODYLIA

BAURUSUCHIDAE

CROCODYLIDAE

DYROSAURIDAE

DINOSAURIA

ANKYLOSAURIDAE

Avisaurus archibaldi

CAENAGNATHIDAE

CARNOSAURIA /

TYRANNOSAURIDAE

CERATOPSIDAE

DROMAEOSAURIDAE

Dryptosaurus aquilunguis

ELMISAURIDAE

HADROSAURIDAE

"HYPHILOPHODONTIDAE"

"IGUANODONTIDAE"

NODOSAURIDAE

ORNITHOMIMIDAE

PACHYCEPHALOSAURIDAE

Pachyrhinosaurus canadensis

PROTOCERATOPSIDAE

SEGNOSAURIDAE

Theselosaurus neglectus

TROODONTIDAE

PTEROSAURIA

AZHDARCHIDAE

PTERANODONTIDAE

ICHTHYOSAURIA

PLATYPTERYGIIDAE

PLESIOSAURIA

ELASMOSAURIDAE

EXPLANATION

- - - - - Possible earlier origin
 — Documented age distribution
 ? — ? Isolated stratigraphic occurrence
 — Known extinction
 — ? Possible extinction
 — Post Paleocene occurrence

Table 2. Marine ages for some important Late Cretaceous and Early Tertiary continental deposits.

Formation	Age (marine standard)	Source(s)
North America		
Denver	late Maastrichtian–early Paleocene	McGookey et al., 1972
“El Gallo”	middle–late Campanian	Morris, 1974
Fox Hills	early–middle Maastrichtian	McGookey et al., 1972
Frenchman	late Maastrichtian	Fox, 1978
Fruitland	middle–late Campanian	Fassett, 1987; Newman, 1987
“Green Sands” (N.J.)	early Maastrichtian	Levin, 1983; Kent et al., 1985, in part
Hell Creek (upper beds)	late Maastrichtian	McGookey et al., 1972
Horseshoe Canyon (=lower Edmonton)	late Campanian–early Maastrichtian Edmonton	Fox, 1978
Javelina	?late Maastrichtian	Mateer, 1981
Judith River	middle Campanian	McGookey et al., 1972; Fox, 1978
Kaiparowits	?late Campanian–early Maastrichtian	Eaton, pers. comm., 1986
Kirtland	late Campanian–early Maastrichtian	Fassett, 1978; Newman, 1987
Laramie (upper beds)	late Maastrichtian	McGookey et al., 1972
Marshalltown/Merchantville/Woodbury	middle–late Campanian	Levin, 1983; Kent et al., 1985, in part
“Mesaverde”	middle Campanian	McGookey et al., 1972
Milk River (upper beds)	early Campanian	Fox, 1978
Moreno	middle–late Maastrichtian	Popenoe et al., 1960
Nacimiento	early Paleocene	Baltz, 1967
Niobrara (upper beds)	early Campanian	McGookey et al., 1972
North Horn (lower beds)	late Campanian–early Maastrichtian	McGookey et al., 1972
Ojo Alamo Sandstone	?early Paleocene	Fassett et al., 1987
Oldman (=upper Belly River)	middle Campanian	McGookey et al., 1972
St. Mary River	late Campanian–early Maastrichtian	McGookey et al., 1972; Fox, 1978
Scollard (=upper Edmonton)	late Maastrichtian	Fox, 1978
Tullock	late Maastrichtian–Danian (early Paleocene)	McGookey et al., 1972
Two Medicine	early–middle Campanian	McGookey et al., 1972; Horner and Makela, 1979
Asia		
Barun Goyot	middle–late Campanian	Fox, 1978
Bayn Shireh	late Cenomanian–early Santonian	Barsbold and Perle, 1980
Boro Khoul beds	?early Campanian	Fox, 1978
Djadokhta (Bayn Dzak)	middle Campanian	Fox, 1978
Khermeen Tsav (red beds I and II)	middle Campanian	Fox, 1978
Nemegt	late Campanian	Fox, 1978
Nogon Tsav	?middle Campanian	Kurzanov, 1976a
Subash	Maastrichtian	Dong, 1977
South America		
Baurú	early Maastrichtian	Steel, 1973
Lecho	late Campanian or early Maastrichtian	Bonaparte and Powell, 1980
San Jorge	?late Maastrichtian	Brett-Surman, 1979

In practice “NALMAs” are biochronologic units without corresponding chronostratigraphic units (time stratigraphic) units, and should be referred to as “intervals” or North American Land Mammal Intervals (NALVIs). NALVIs are informal units, which are near equivalents to the Oppel-zone and assemblage zones recognized by the International Sub-

commission on Stratigraphic Classification (1976:50, 57). These vertebrate-bearing horizons, which are largely based on discontinuous local faunas, do not, and cannot, cover all of Cenozoic and Late Cretaceous time, contrary to the opinions of Wood et al. (1941) and Lillegraven and McKenna (1986). NALVIs are definable by an aggregate of fossil taxa,

whose intervals of time vary in duration, as expressed solely by the physical extent of the interval fauna in a particular stratigraphic sequence. Because many formations are known to be time-transgressive, only that part of the stratigraphic

unit that bears the interval fauna, can be assigned a relative "age." Formal age assignment of these intervals is made to the standard ages which are recognized by most biostratigraphers and paleontologists.

REVIEW OF THE CRETACEOUS–TERTIARY BOUNDARY REPTILIAN TAXA

CHELONIA (TESTUDINES)

Chelonia is probably the most poorly studied reptilian group, at least at the generic, species, and subspecies level, that encounters the K–T boundary. The number of valid species and the diversity among the different families of chelonians are not precisely known owing to the fact that these reptiles have not received much attention because of problems in carapace/plastron–skull associations and intraspecific carapace/plastron variations. Recent studies by Hutchison and Archibald (1984, 1986) demonstrate that of the large number of turtle genera and subgenera in the Hell Creek and Tullock formations (late Maastrichtian–earliest Paleocene) of Montana, nearly three-fourths of the taxa cross the Cretaceous–Tertiary boundary. For this study I follow the classification of Gaffney (1975) for the families of turtles.

BAENIDAE. The family Baenidae is represented by a number of taxa that span the K–T boundary only to become extinct by late Eocene time (Gaffney, 1972). The baenid *Palatobaena bairdi* has been reported from the Late Cretaceous (late Maastrichtian) of Montana, from the earliest Paleocene of Colorado and New Mexico, late-early Paleocene of Montana, and the early Eocene of Wyoming (Archibald and Hutchison, 1979; Gaffney, 1972; Sullivan and Lucas, 1986). *Compsemys victa* is known solely from shells from the Late Cretaceous (Maastrichtian) through late-early Paleocene (Gaffney, 1972). *Neurankylus* cf. *N. eximius* is known from both Late Cretaceous and early Paleocene deposits of Montana and New Mexico (Hutchison and Archibald, 1986; Sullivan and Lucas, 1986; Sullivan et al., unpublished manuscript). *Plesiobaena* is known by two species and the genus ranges from the Late Cretaceous (Maastrichtian) through the early Paleocene. The stratigraphic ranges of other baenid species through the K–T transition are not known with certainty.

CHELONIIDAE. The sea turtle family Cheloniidae first appears in the Late Jurassic and ranges to the Recent (Mlynarski, 1976). Numerous genera have been named (Zangerl, 1980, recognizes some 16 "better known" genera and 20 species) all of which have limited stratigraphic occurrences on both sides of the K–T boundary. While it appears that the species have changed, the taxonomic diversity of species has remained relatively constant through much of Late Mesozoic and Cenozoic time.

DERMATEMYDIDAE. Dermatemydids first appear in the Cretaceous (Gaffney, 1975), although an occurrence of the species *Tretosternon bakewelli*, from the Purbeck and Wealden beds suggests a Late Jurassic origin for this family (Mlynarski, 1976). The genus *Adocus* is known from strata

of Late Cretaceous (Maastrichtian) through middle Eocene of North America. The species diversity of *Adocus* is not known and the genus is in need of revision (Sullivan and Lucas, 1986). Other dermatemydids such as *Basilemys*, need to be re-evaluated with respect to their specific taxonomy. The Recent dermatemydids are represented by the genus *Dermatemys*.

EMYDIDAE. Contrary to Russell's (1975, 1982d) diagrams, there is no documented occurrence of a member of the turtle family Emydidae prior to Paleocene time (Gaffney, 1975; Mlynarski, 1976). This family is restricted to the Cenozoic and is not considered further.

PELOMEDUSIDAE. Two pelomedusid genera, *Podocnemis* and *Taphrosphys*, cross the Cretaceous–Tertiary boundary. *Podocnemis* has a wide geographic range (South America, Africa [and Madagascar?], Europe, and Asia) suggesting that antiquity of this genus extends back to earlier Mesozoic time. *Podocnemis* is known only by six species (Mlynarski, 1976). *Taphrosphys sulcatus* is a cosmopolitan pelomedusid species that is known from the Late Cretaceous through Miocene of North and South America, and from the Eocene through Miocene of Africa. Other genera of pelomedusids occur in the middle and upper Tertiary strata of the Old World and range to the Recent (Mlynarski, 1976).

PROTOSTEGIDAE. The extinct family Protostegidae includes five genera of Campanian marine turtles (*Archelon*, *Calcarichelys*, *Chelosphargis*, *Protostega*, and *Rhinochelys*), which are in turn represented by nine species. The youngest occurrence of any of these taxa is from late Campanian strata (Zangerl, 1953a). The family Protostegidae, as correctly presented by Russell (1975, 1982d), became extinct prior to the Maastrichtian and hence the K–T boundary.

TOXOCHELYIDAE. The sea turtles belonging to the family Toxochelyidae are known from strata of Early Cretaceous (Coniacian) age and successfully cross the K–T boundary where their last recorded occurrence is in strata of Eocene age (Zangerl, 1953b, 1980). Zangerl (1980) recognized 11 genera and 23 species distributed among three subfamilies, one of which (the Lophochelyinae) is restricted to the Late Cretaceous, and experienced major reduction in species prior to the late Maastrichtian. The subfamily Toxochelyinae is known by *Toxochelys latiremis* and *Porthochelys laticeps* (late Coniacian); *Toxochelys moorevillensis* and *Thiochelys lapissossea* (early Campanian); *Toxochelys barberi* and *T. browni* (late Campanian); and *T. weeksi* (early Maastrichtian). The species *Dollochelys atlantica* and *D. casieri* are from the late Maastrichtian and early Eocene, respectively. The subfamily Lophochelyinae is known by five late Campanian species:

Lophochelys niobrarae, *L. natatrix*, *Ctenochelys stenopora*, *C. procax*, and *Prionochelys galeotergum*; four early Campanian species: *Lophochelys venatrix*, *Ctenochelys tenuitesta*, *C. acris*, and *Prionochelys matutina*; the species *P. nauta* is from late Campanian strata (Marlbrook Marl of Arkansas) and *Pertreus ornatus* is known with certainty from middle and late Maastrichtian strata with a probable occurrence in the early Maastrichtian. The validity of these Late Cretaceous species is not clear. The subfamily Osteopyginae consists of three taxa: *Osteopygis emarginatus* from the middle and late Maastrichtian, *Erquelinnesia grosselti* from the early Eocene, and *Glossochelys planimenta* from the middle Eocene London Clay (Zangerl, 1980).

TRIONYCHIDAE. *Trionyx*, known from numerous fossil "species" (many of which are certainly not valid) that range from the Late Jurassic to Recent time (Młynarski, 1976). The taxonomic diversity of this genus cannot be assessed pending revision of this taxon. *Trionyx*, including here *Aspideretes*, *Amyda*, and *Platyptelis*, crosses the K–T boundary.

EOSUCHIA

CHAMPSOSAURIDAE. The family Champsosauridae consists of only two genera, the North American genus *Champsosaurus*, which crosses the K–T boundary, spanning the middle Campanian–early late Paleocene and *Simoedosaurus* known from the early Paleocene of Europe and North America (Sigogneau-Russell, 1975; Sigogneau-Russell and Baird, 1978). Six species of *Champsosaurus* are currently recognized (Erickson, 1972, 1981) only one of which (*C. laramiensis*) occurs in strata on both sides of the K–T boundary. All other *Champsosaurus* species have restricted stratigraphic occurrences above and below the K–T boundary (Erickson, 1972, 1981; Bryant, pers. comm., 1985).

LACERTILIA

Our knowledge of the terrestrial lizard families and their stratigraphic distribution has been revised significantly since Russell's (1975, 1982d) reviews of reptilian taxonomic diversity, principally by the works of Estes (1983a, 1983b) and a subsequent paper by Borsuk-Bialynicka (1984). Of the ten lizard families listed by Russell (1975, 1982d) only six are consistent with recent interpretations by Estes (1983a, 1983b) and three additional taxa, two of them new, have been recently reported to be of Late Cretaceous age (Borsuk-Bialynicka, 1984). The lizard family Xantusiidae, contrary to the diagrams presented by Russell (1975, 1982d), is not known from strata earlier than late-early Paleocene (Estes, 1983b; Sullivan, 1982) and is first indicated by the species *Palaeoxantusia fera*. Owing to the fact that xantusiids are not known from Upper Cretaceous deposits, this family does not concern us here. In addition, the family "Amphisbaenidae" listed by Russell (1975, 1982d) is treated here in its own section Amphisbaenia (below).

AGAMIDAE. *Mimeosaurus crassus* was the first fossil agamid lizard reported from Bayn Dzak locality, Djadokhta Formation, Mongolian People's Republic (Gilmore, 1943;

Estes, 1983b). Borsuk-Bialynicka and Moody (1984) recently named two additional agamids, *Priscagama gobiensis* and *Pleurodontagama aenigmatodes* from the Djadokhta Formation and the red beds of Khermeen Tsav, Mongolian People's Republic. The family Agamidae is known by a few Eocene genera and by extant taxa (Estes, 1983b). The group ranges from the middle Campanian to Recent and successfully crossed the Cretaceous–Tertiary boundary.

ANGUIDAE. The Anguidae has left the best fossil record of any terrestrial lizard family, being well represented in rocks of late Paleocene–late Oligocene age, principally by the subfamily Glyptosaurinae (Sullivan, 1979; Gauthier, 1982; Estes, 1983b). The oldest known anguid lizard is *Odaxosaurus piger* from the middle Campanian "Mesaverde," Fruitland and Judith River formations (Estes, 1983b). The earliest "anguine" *Machaerosaurus torreonensis* occurs in the late-early Paleocene of New Mexico and Wyoming (Estes, 1983b; Gilmore, 1928; Sullivan, 1981, 1982). *Apodosaurus minutus* from the early Eocene of Wyoming is the earliest member of the subfamily Anniellinae (Gauthier, 1982). Contrary to what has been previously thought, new data presented by Good (in press) demonstrate that the subfamily Gerrhonotinae originated late in Tertiary time, not in the Late Cretaceous as reported by Estes (1964) and Armstrong-Ziegler (1980). The earliest diploglossine was recently reported by Gauthier (1982) from the early Eocene of Wyoming. Suffice it to say that the Anguidae crossed the K–T boundary, began to diversify in the early Paleocene, and is today represented by all the aforementioned subfamilies, save the Glyptosaurinae, which became extinct at the end of the Oligocene epoch (Sullivan, 1979).

Bainguis parvus. Borsuk-Bialynicka (1984) established the monotypic lizard family "Bainguidae" for the species *Bainguis parvus* from the Barun Goyot Formation, Mongolian People's Republic. Since this family is based on a monotypic taxon, the family rank is redundant and unnecessary. The range of *B. parvus* is restricted to the middle Campanian and cannot be commented on further.

HELODERMATIDAE. The lizard family Helodermatidae has a poor fossil record. The earliest definite helodermatid is from the late Paleocene of North America with the occurrence of cf. *Eurheloderma* (Pregill et al., 1986). *Paraderma bogerti* is a problematic helodermatid, and the range of the Helodermatidae probably extends into the late Maastrichtian Lance Formation (Estes, 1983b; Pregill et al., 1986). Helodermatid lizards are known to include six taxa, two of which are extant species.

IGUANIDAE. Iguanid lizards first appear in the early Maastrichtian Baurú Formation, Brazil, being represented by the species *Pristiguana brasiliensis* (Estes and Price, 1973; Estes, 1983b). In North America, the earliest recorded occurrence for the family Iguanidae is possibly *Swainignuonoides milleri* from the late-early Paleocene "Fort Union Formation" (Sullivan, 1982) and the early Eocene San José Formation (Sullivan and Lucas, in press). The Iguanidae ranges from the early Maastrichtian to the present, and is represented by numerous extant taxa.

LANTHANOTIDAE. Borsuk-Bialynicka (1984) recently

extended the range of the lizard family Lanthanotidae back to the middle Campanian based on the occurrence of the lizard *Cherminotus longifrons* from the Barun Goyot Formation, Mongolian People's Republic.

MOSASAURIDAE. Only one family of aquatic varanoids, the Mosasauridae, survived into the Late Cretaceous, the Aigialosauridae and Dolichosauridae having become extinct by Turonian time (Russell, 1967). The Mosasauridae is known to range only up to the early Maastrichtian. A problematic occurrence of a mosasaur tooth identified by Gilmore from the early-middle Maastrichtian Fox Hills Sandstone is probably reworked from the underlying Pierre Shale (Leonard, 1912). Russell (1975) reported late Maastrichtian mosasaurs from Belgium, however re-evaluation of the chronostratigraphic position of these Late Cretaceous units demonstrates that the upper part of the Maastrichtian is *not* present, strongly suggesting that the mosasaurs are older (Robaszyński, 1979). Mosasaur occurrences have been reported from the Late Cretaceous units in eastern North America, but these strata are believed to be pre-late Maastrichtian in age (Levin, 1983).

NECROSAURIDAE. The "Parasaniwidae" listed by Russell (1975, 1982d) is presently recognized as a subfamily within the lizard family Necrosauridae (not listed by Russell, 1975, 1982d) (Estes, 1983b). The oldest member of the subfamily Parasaniwinae is *Parasaniwa wyomingensis* from the late Maastrichtian Lance and Hell Creek formations of Wyoming and Montana (Estes, 1983b). Hecht (1959) and McKenna (1960) both reported *Parasaniwa* sp. from the early Eocene of western North America. However, Estes (1983b) indicated that the specimens upon which this lizard occurrence is based may represent another taxon. It is unclear as to whether or not *Parasaniwa* ranged into the early Eocene of North America. Regardless, the Necrosauridae is known from the late Maastrichtian through late Eocene, at which time this family became extinct.

Paravaranus angustifrons. Another monotypic lizard family "Paravaranidae" was established by Borsuk-Bialynicka (1984) for the species *Paravaranus angustifrons* from the Barun Goyot Formation, Mongolian People's Republic. As with "Bainiuidae" (above), family rank is unwarranted, because the taxon is monotypic. The stratigraphic range of *P. angustifrons* is restricted to the middle Campanian.

SCINCIDAE. *Contogenys sloani* from the late Maastrichtian and late-early Paleocene of North America (Estes, 1983b) traversed the K-T boundary unaffected and is the first species to represent the family Scincidae. The Scincidae is a diverse lizard family that proliferated in the Tertiary and is known by many Recent taxa (Estes, 1983b). Contrary to Russell (1975, 1982d), scincids are not known from Campanian age sediments.

TEIIDAE. The "Polyglyphanodontidae" listed by Russell (1975, 1982d) is currently recognized as a subfamily (Polyglyphanodontinae) within the lizard family Teiidae (Estes, 1983b) and is first represented by the species *Adamisaurus magnidentatus* from the middle Campanian Barun Goyot Formation, Djadokhta Formation, and from the red beds of Khormeen Tsav, Mongolian People's Republic. Four addi-

tional teiid genera (*Cherminisaurus*, *Darchansaurus*, *Erdenesaurus*, *Macrocephalosaurus*) belonging to the Polyglyphanodontinae, totaling seven species, are all from middle Campanian strata from the Mongolian People's Republic (Estes, 1983b). In North America, the polyglyphanodontines are represented by four species: *Haptosphenus placodon* from the Lance and Hell Creek formations of Wyoming and Montana, respectively; *Paraglyphanodon utahensis*, and *P. gazini* from the North Horn Formation of Utah, and *Polyglyphanodon sternbergii* from the North Horn Formation and from the "El Gallo Formation," Baja California (Estes, 1983b). The earliest teiine from North America is *Leptochamops denticulatus* from the middle Campanian Fruitland Formation, New Mexico (Estes, 1983b). The other taxon, also known from the Fruitland Formation, is *Chamops segnis* (Estes, 1983b; Sullivan, 1981). The family Teiidae is well established in both Asia and North America prior to the Cretaceous-Tertiary transition. While the polyglyphanodontines of the Late Cretaceous do not extend beyond the K-T boundary, their highest stratigraphic occurrence is in the North Horn Formation (late Campanian-early Maastrichtian). The family Teiidae, represented by species within the subfamily Teiinae, continued to proliferate during the Cenozoic in South America (Estes, 1983b).

VARANIDAE. The Varanidae is first represented by the occurrence of *Palaeosaniwa canadensis* from the Oldman Formation, Alberta, Canada. Occurrences of *P. canadensis* and cf. *P. canadensis* from the late Maastrichtian and late-early Paleocene, respectively (Estes, 1983b; Sullivan, 1982) suggest that this species traversed the K-T boundary. The family Varanidae is known by many extant species.

XENOSAURIDAE. *Exostinus lancensis* has been reported from the late Maastrichtian Lance and Hell Creek formations and the "Fort Union Formation," late-early Paleocene of western North America (Estes, 1964, 1983b; Gilmore, 1928; Sullivan, 1982), thus successfully crossing the K-T boundary. Again, Russell (1975, 1982d) indicated an earlier (Campanian) occurrence for the Xenosauridae which is not supported by published accounts. The Xenosauridae extends to the Recent and is known by species of *Xenosaurus* and *Shinisaurus* (Estes, 1983b).

AMPHISBAENIA

Russell (1975, 1982d) listed the order Amphisbaenia as a family (Amphisbaenidae) within the lizards. I follow Estes (1983b) recognizing this group at the ordinal level. Regardless, Russell (1975, 1982d) diagrammed the amphisbaenians as being basal Paleocene in occurrence. No amphisbaenians are known from the earliest Paleocene. The oldest amphisbaenian is *Plesiorhineura tsentasi*, a member of the amphisbaenian family Rhineuridae, that was recently reported from the late-early Paleocene of New Mexico (Sullivan, 1985). Since *Plesiorhineura* first appears in post-Cretaceous strata it has little relevance with respect to the K-T boundary, although it is quite feasible that the family Rhineuridae originated in Late Cretaceous or earliest Paleocene time.

SERPENTES

ANILIIDAE. Snakes are rare in the fossil record and are known principally from disarticulated vertebrae. Nevertheless, snakes have been reported in Late Cretaceous and early Tertiary strata (Gilmore, 1938; Hoffstetter, 1955; Estes, 1964; Estes et al., 1969; Estes and Berberian, 1980; Holman, 1979; Rage, 1984; and Sullivan and Lucas, in press). Estes (1964) reported that the family Aniliidae, based on material referred to the snake *Coniophis precedens*, was present in the late Maastrichtian and Hecht (1959) has recorded this taxon in the middle Eocene. "*Coniophis*" *cosgriffi* has been reported in the Fruitland Formation, New Mexico (Armstrong-Ziegler, 1978, 1980), but this species belongs to the family Boidae (Rage, 1984; Estes and Báez, 1985). The Aniliidae ranges from the late Maastrichtian to Recent.

BOIDAE. A single trunk vertebra of the large bold *Madtsoia madagascariensis* from the "Gîte du Guide" (?Santonian or ?Campanian) North of Berivotra, Madagascar, is the oldest occurrence of this family (D. Russell et al., 1976; Rage, 1984). "*Coniophis*" *cosgriffi* from the middle Campanian of New Mexico (above), is the only North American Cretaceous boid known. The henophidian snake *Helagras prisciformis* is known by trunk vertebrae from the Paleocene of New Mexico and the late-early Paleocene of Wyoming (Gilmore, 1938; Holman, 1979; Rage, 1984). *Helagras* has been inferred to be a member of the family Boidae (Hoffstetter, 1955; Hoffstetter and Rage, 1972; Rage, 1984) but Holman (1983) believes that reference to the Boidae is questionable and thus prefers to place it in *Henophidia incertae sedis*.

Russell (1975, 1982d) in his diagrams indicated the presence of the family Boidae in the Late Cretaceous based on a specimen referable to "*Coniophis*" *cosgriffi* originally reported by Estes and Berberian (1970) and later by Estes and Báez (1985). Like the Aniliidae, the Boidae has a Late Cretaceous origin, crossed the K-T boundary, and proliferated in the Paleogene.

Dinilysia patagonia. *Dinilysia patagonia* from the Late Cretaceous of South America, has been interpreted as being close to Anilioidea (Estes et al., 1970) while Rage (1984) believes it shares affinities with the Booidea. Previously, this snake had been included in its own subfamily Dinilysiniace by Romer (1956). Estes et al. (1970) referred *Dinilysia* to basal Booidea without designating a specific familial designation. Estes (pers. comm., 1985) believes *Dinilysia* is a monotypic taxon, which is followed here. *Dinilysia patagonia* is restricted to the middle Campanian.

CROCODYLIA

Five families of crocodilians were cited in Russell's (1975) diagram, but he only recognized four families in his revised diagram (Russell, 1982d). The sebecosuchian family Sebecidae, a small South American crocodilian family erroneously presented in Russell's (1975) diagram for North America, is known by two species *Sebecus icaeorhinus* and *S. huilensis*, which are restricted to Paleogene and upper Miocene strata

(Steel, 1973; Buffetaut, 1982). The mesosuchian family Goniopholidae is represented by species that are known principally from the early Maastrichtian "Greensands" of New Jersey (North America), rather than latest late Maastrichtian as implied by Russell (1975). Finally, the mesosuchian family Pholiosauridae, as Russell has correctly indicated in his 1975 diagram, became extinct well before the K-T boundary (late Santonian). Suffice it to say that none of these three crocodilian families reaches the K-T boundary.

BAURUSUCHIDAE. The sebecosuchian family Baurusuchidae ranges from the Late Cretaceous (early Maastrichtian) of South America through the Eocene of North America and Europe and is known by five monotypic genera (Steel, 1973). This family traverses the K-T boundary without a decrease in species diversity.

CROCODYLIDAE. The eusuchian families Crocodylidae and the "Alligatoridae" listed by Russell (1975) are treated here as one family, the Crocodylidae, following Steel (1973). *Brachychampsa montana* has been reported from the Kirtland and Judith River formations of New Mexico and Montana, respectively, and *Brachychampsa* sp. has recently been discovered in the late Maastrichtian Hell Creek Formation, North Dakota (Hutchison, pers. comm., 1986). The genus *Crocodylus* is known by a plethora of species (many of which are probably not valid) that span Early Cretaceous to Recent time (Steel, 1973). *Deinosuchus* (= *Phobosuchus*) *hatcheri* is from the Judith River Formation, Montana, and *D. riograndensis* is from the Agüa Formation, Texas; both are from strata that are pre-late Maastrichtian. Three species of the North American taxon *Leidyosuchus* are valid: *L. canadensis*, from strata of middle Campanian to late Maastrichtian age; *L. acutidentatus* from the early Paleocene (Danian) strata; and *L. riggsi* from the late Paleocene (Selandian) strata (Lucas and Sullivan, 1986). The South American taxon *Necrosuchus ionesis* from the Salamanca Formation, Chubut, Patagonia, is considered pre-late Maastrichtian. Species diversity of other taxa near the Cretaceous-Tertiary boundary (i.e., *Allognathosuchus* [which includes *Navajosuchus novomexicanus* and *Wannaganosuchus brachymanus*, etc., Sullivan et al., in press]) are not well known owing to their incomplete nature. Russell's tabulation of numerous crocodilian specimens in museum collections does not reflect species diversity of crocodilians as previously indicated, because they suffer from the same collecting biases as the chelonians, and from lack of study by vertebrate paleontologists.

DYROSAURIDAE. The extinct, and predominately African, mesosuchian crocodilian family Dyrosauridae (includes the "Congosauridae" of Steel, 1973) is known by several genera (*Atlantosuchus*, *Dyrosaurus*, *Hyposaurus*, *Phosphatosaurus*, *Rhabdognathus*, *Sokotosuchus*, *Tilemsisuchus*) and an unresolved number of species, varying in age from Maastrichtian through Eocene, and widely distributed in North Africa, New Jersey, Brazil, and Pakistan (Storrs, 1986). Although the members of this family are poorly known, their stratigraphic distribution demonstrates that taxa in this group successfully crossed the K-T boundary.

DINOSAURIA

Dinosaurs have recently been demonstrated to be a monophyletic group by Gauthier (1986) based on characters of the manus, ilium, cervical vertebrae (axis-atlas complex), and other features, thus eliminating the traditional dichotomy of the orders Saurischia and Ornithischia as the two predominant taxonomic categories for these reptiles (Figure 1). I follow Gauthier's classification, rather than that of Paul (1984a), in my range chart for the reptilian families (Table 1). I also follow Gauthier (1986) and Cracraft (1986) in recognizing the "Aves" and other "bird" taxa as members of the Theropoda (hence Dinosauria). I restrict my presentation to the traditional dinosaurian classification scheme for this paper by omitting these taxa from my chart (Table 1) so that comparisons can readily be made with the works of Russell (1975, 1982d). The recognition of related "bird" taxa, as members of the Dinosauria, only further demonstrates the gradualistic nature of the K-T transition in terms of reptilian species. Dinosaurian families and other taxa discussed immediately below include only those families that have been cited by workers as reaching or approaching the Cretaceous-Tertiary boundary.

Russell (1975) listed 11 dinosaurian families in his diagram and in his subsequent chart (Russell, 1982d) listed 15 dinosaurian families for an apparent net gain of four families to further lend support for an abrupt mass extinction event. Russell's (1982d) chart included five "new" dinosaurian families: Ankylosauridae, "Dryptosauridae," Oviraptoridae (included here in the Caenagnathidae), Saurornithoididae, and "Thescelosauridae" (which are discussed below). These "newly" recognized families do not affect species diversity because they only represent a reorganization of previously known species. Two of the dinosaurian families listed by Russell (1975), the Troodontidae and the family Nodosauridae have been since redefined; the former includes the dinosaur family "Saurornithoididae" and other taxa and the latter family includes some of the species that are now assigned to the Ankylosauridae, a family that is distinct from the nodosaurids (see below).

In a more recent paper on dinosaurs from North America, Russell (1984) lists two dinosaur families: the "tooth taxon" "Aublysodontidae" (Carpenter, 1982), which is treated here as Theropoda *incertae sedis* and the rather surprisingly late occurrence of the sauropodomorph family Diplodocidae which is based solely on a single vertebra (of "Morrison aspect") and is possibly reworked (McIntosh, pers. comm., 1985).

ANKYLOSAURIDAE. Originally not appearing in Russell's (1975) chart of reptilian diversity, this family is included by Russell (1982d) presumably based on the revision of the Ankylosauria presented by Coombs (1978). Coombs recognized two families of ankylosaurians, the Ankylosauridae and the Nodosauridae (see below). The family Ankylosauridae includes ten Late Cretaceous species, the majority of which are pre-late Maastrichtian in age: *Amtosaurus mag-*

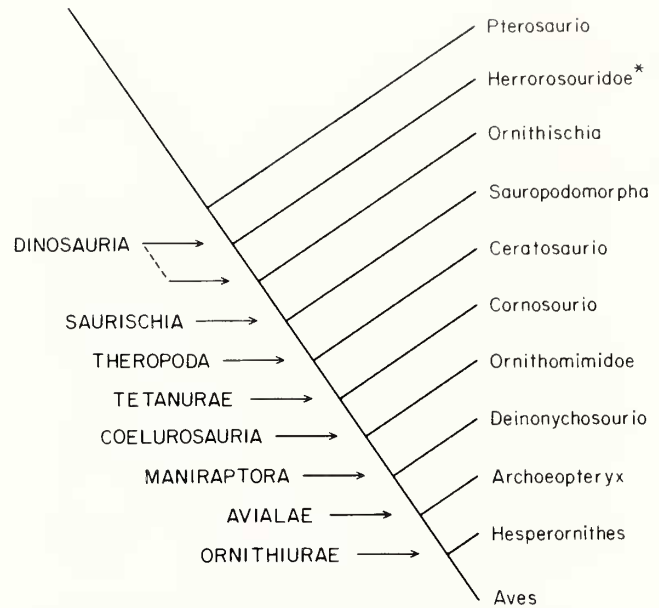


Figure 1. Cladistic hypothesis for the Dinosauria proposed by Gauthier (1986) and followed here. Asterisk denotes metataxon (see Gauthier, 1986, for discussion).

nus, *Ankylosaurus magniventris*, *Euoplocephalus tutus*, *La-metasaurus indicus*, *Pinacosaurus grangeri*, *Saichania chul-sanensis*, *Talarurus disparoservatus*, *T. plicatospineus*, *Tarchia kielanae*, and *T. gigantea* (Maryńska, 1977; Coombs, 1978; Kurzanov and Tumanova, 1978; Tumanova, 1981). The Asian ankylosaurs are all from pre-Maastrichtian deposits. These include *Pinacosaurus* from the Djadokhta Formation, *Saichania* from the Barun Goyot Formation, and *Talarurus* from the Bayn Shireh "formation," all of which are from the Mongolian People's Republic (Gradziński et al., 1977; Maryńska, 1977).

Euoplocephalus tutus is known from the Judith River, Two Medicine, Horseshoe Canyon, and Oldman formations of Alberta. *Ankylosaurus magniventris*, the latest surviving ankylosaurid, is known by three specimens from the Hell Creek and Scollard formations, and is late Maastrichtian in age (Coombs, 1978). Furthermore, *Ankylosaurus magniventris* is the only ankylosaurian, from either the Ankylosauridae or Nodosauridae, that is known from "Lancian" or late Maastrichtian age deposits.

***Avisaurus archibaldi*.** Brett-Surman and Paul (1985) recently proposed the family "Avisauridae" for the new species *Avisaurus archibaldi* based on a right metatarsus from the Hell Creek Formation and two other metatarsi, one from the Lecho Formation of Argentina, and another from the Hell Creek Formation of Montana, which they believe to be distinct, based on "uniquely divergent morphology." However, the primitive nature of these metatarsi compared to those of *Archaeopteryx* and other avian taxa, as indicated by their incomplete fusion distally, suggests that *Avisaurus* may rep-

resent a derived dromaeosaurid. However, for the present I consider the species *Avisaurus archibaldi* to be *Coelurosauria incertae sedis*.

CAENAGNATHIDAE. Originally established by Sternberg (1940) for the reception of the species *Caenagnathus collinsi*, the Caenagnathidae was believed to be a new family of birds. This taxon has had a history of being tossed back and forth from the traditional "Aves" to Reptilia (see Cracraft, 1971) and is now recognized as a group of coelurosaurian theropods (Gauthier, 1986). The family includes three taxa: *Caenagnathus collinsi* and *C. sternbergi* both from the Horseshoe Canyon Formation, Alberta (see Cracraft, 1971) and *Oviraptor philoceratops* from the Djadokhta Formation, Mongolian People's Republic. *Oviraptor* sp. has been reported from the middle Campanian red beds of Khermeen Tsav I and II (Gradziński et al., 1977). As such, this family is restricted to the middle Campanian and has been included in *Coelurosauria incertae sedis* by Gauthier (1986).

Russell (1982d) indicated that the family Oviraptoridae, a monotypic family that is included here in the Caenagnathidae (see Barsbold, 1983; Gauthier, 1986), ranges from the early Campanian to the late Maastrichtian. However, I know of no documented occurrence of any of the above-mentioned taxa that would support an occurrence younger than middle Campanian.

CARNOSAURIA/TYRANNOSAURIDAE. Gauthier (1986) recognized only five taxa that Russell (1970) included in the family Tyrannosauridae: *Albertosaurus sarcophagus* from the Horseshoe Canyon Formation, Alberta; *A. lancensis* from the Lance Formation, Wyoming; *A. libratus* from the Oldman Formation, Alberta; the monotypic genera *Tarbosaurus bataar* from the "Edmontonian age" (late Campanian-early Maastrichtian) strata of the Nemegt Basin, Mongolian People's Republic; and *Tyrannosaurus rex* from the "Laramie" and Hell Creek formations, Montana. *Tyrannosaurus rex* and *Albertosaurus lancensis* are the latest surviving taxa of the family Tyrannosauridae, and are also the latest surviving carnosaurs, a group that consisted of a number of species that ranged from the Late Jurassic to Late Cretaceous and consisted of 13 valid taxa (Gauthier, 1986).

Daspletosaurus torosus from the Horseshoe Canyon Formation, Alberta, which was included in the Tyrannosauridae by Russell (1970), has been removed from the Tyrannosauridae by Gauthier (1986) and placed within the Carnosauria. A number of carnosaurian (including "teratosaurids" and "megalosaurids") taxa, too numerous to list here, are known mostly from pre-Maastrichtian deposits. The more important taxa include: *Allosaurus fragilis*, from the Late Jurassic Morrison Formation; *Acrocanthosaurus atokensis* from the Early Cretaceous Trinity Sands; *Alectrosaurus olseni* from the Cenomanian Iren Dabasu Formation, People's Republic of China; *Alioramus remotus* from the middle Campanian Nogon Tsav, Mongolian People's Republic (Kurzanov, 1976a); *Chingkandousaurus fragilis* from "Upper Cretaceous strata in a place south of Chingkankou," People's Republic of China (see Young, 1958:101); *Dryptosaurus aquilunguis* from the early Maastrichtian "Greensands" of

New Jersey (see below); *Spinosaurus aegypticus* from "Upper Cretaceous deposits" (early Cenomanian) of Egypt; *Indosaurus* (= *Orthogoniosaurus*) *matleyi* and *Indosuchus raptorius* from the "Late Cretaceous" (Turonian, Santonian or Maastrichtian, see Chatterjee, 1978; ?Campanian, Chatterjee, pers. comm., 1985) of Madhya Pradesh, India; *Itemirus medullaris* from the late Turonian Central Kyzylkum sands of Soviet Central Asia (Kurzanov, 1976b); and *Majungasaurus crenatissimus* from the Campanian "Gîte du Guide" of Madagascar (D. Russell et al., 1976). Clearly carnosaurs show a decline in species before the late Maastrichtian, contrary to Russell (1975).

CERATOPSIDAE. Only two valid genera of ceratopsids are known to occur in late Maastrichtian (Lance equivalent) deposits, *Torosaurus* and *Triceratops* (= *Agathaumys*). The former is a rare ceratopsid known by one species, *Torosaurus latus* from the uppermost part of the Lance Formation, above the stratigraphic occurrence of the abundant ceratopsid *Triceratops* (Steel, 1969). The species *Torosaurus* (= *Arrhinoceratops*) *utahensis* (Lawson, 1976) is believed to be a precursor of *T. latus*. Cobabe and Fastovsky (1987) named *Ogrosaurus olsoni*, from the late Maastrichtian Hell Creek Formation, but because this taxon is based on a very fragmentary specimen, and because it may be a junior synonym of *Triceratops*, it is viewed as a *nomen dubium*. Numerous species of the genus *Triceratops* have been named, many of which are invalid or synonyms. Sloan (1985) reported that five species appear to be valid (*T. horridus*, *T. prorsus*, *T. elatus*, and *T. obtusus*), and Paul (pers. comm., 1986) reported that only two species of *Triceratops* are valid based on the shape of the premaxillary region. Ostrom and Wellnhofer (1986) recently suggested that the genus *Triceratops* is monotypic, represented by the sole species *T. horridus*, a view that is accepted here. Therefore, *Torosaurus latus* and *Triceratops horridus* are the last and only two late Maastrichtian ceratopsid species, antedated by numerous species belonging to the genera *Anchiceratops*, *Arrhinoceratops*, *Avaceratops*, *Brachyceratops*, *Centrosaurus*, *Ceratops*, *Chasmosaurus*, *Eoceratops*, *Monoclonius*, *Pentaceratops*, *Styracosaurus* (species too numerous to list here and many of which most certainly are not valid, see Dodson, 1986, for discussion), strongly supporting a major decline in ceratopsid taxa prior to the late Maastrichtian. Russell (1975, 1982d) diagrammed the Ceratopsidae from the early Campanian through late Maastrichtian. Based on *Monoclonius crassus*, "*Ceratops*" (?= *Chasmosaurus*) *montanus*, and *Avaceratops lammersi* from the Judith River Formation, the oldest documented occurrence of a ceratopsid (*sensu* this study) is middle Campanian. The stratigraphic range of the Ceratopsidae is middle Campanian to late Maastrichtian.

DROMAEOSAURIDAE. Four taxa are recognized by Gauthier (1986) in the family Dromaeosauridae: *Adasaurus mongoliensis* from the Khara Khutul locality (Cenomanian), southeast Mongolia (Barsbold, 1983); *Deinonychus antirrhopus* from the Coverly Formation (late Aptian), Montana; *Dromaeosaurus albertensis* from the Horseshoe Canyon Formation, Alberta; and *Velociraptor mongoliensis* from the beds

of Toogreeg and the Djadokhta Formation, Mongolian People's Republic. *Velociraptor* sp. has been reported from the Khulsan, Barun Goyot Formation, the red beds of Khermeen Tsav I and the Nemegt Formation, Mongolian People's Republic (Gradziński et al., 1977). Paul (1984a) believes that both *Deinonychus* and *Saurornitholestes* (Sues, 1978) are congeneric with *Velociraptor*. Gauthier (1986) includes *Saurornitholestes langstoni* within *Coelurosauria incertae sedis*. Ostrom (1969) reported the stratigraphic range for the Dromaeosauridae as being late Aptian to late Campanian to early Maastrichtian. Russell (1975, 1982d, 1984) reported that the family extends to the late Maastrichtian based upon the inclusion of the "tooth taxon" *Paronychodon lacustris* and an occurrence of cf. *Dromaeosaurus* sp. Because phylogenetic relationships of the former genus remain unclear, assignment to this family is far from certain and thus the presence of the family Dromaeosauridae in late Maastrichtian strata is doubtful. None of the aforementioned valid taxa are known to occur in strata younger than early Maastrichtian (see Steel, 1970), therefore Ostrom's (1969) range for the Dromaeosauridae stands as correct unless *Avisaurus archibaldi* proves to be an advanced dromaeosaurid (see *Avisaurus* above).

"DEINOCHEIRIDAE." This family is not recognized here because it is included within the family Ornithomimidae (Gauthier, 1986).

***Dryptosaurus aquilunguis*.** The "Dryptosauridae" (Marsh, 1890:424) was cited by Russell (1982d) for the species *Dryptosaurus aquilunguis*, a family not recognized by Gauthier (1986) because it is monotypic. Gauthier (1986) interpreted *D. aquilunguis* as being intermediate between the family Tyrannosauridae and the genus *Allosaurus*, and thus belongs to the large taxon, Carnosauria. The transitional nature of this carnosaur taxon probably accounts for its past inclusion in the family "Megalosauridae." The youngest known occurrence of *Dryptosaurus aquilunguis* is in the early Maastrichtian "Greensands" (=Mt. Laurel, Navesink, and New Egypt formations) of New Jersey and Delaware (Horner, 1979), and thus is pre-late Maastrichtian. Russell (1982d) illustrated the range of this monophyletic family as early to late Maastrichtian. Because *Dryptosaurus* is only one of many carnosaurs known from the Mesozoic, real diversity of carnosaur taxa can only be assessed by the number of carnosaur species (*sensu* Gauthier, 1986) through time, rather than by monotypic families and families such as the Tyrannosauridae that include a small number of species (see Carnosauria/Tyrannosauridae, above). Lastly, some isolated teeth have been attributed to the genus *Dryptosaurus* (Estes, 1964) may represent a juvenile or subadult carnosaur such as *Tyrannosaurus rex*.

ELMISAURIDAE. Not recognized by Russell (1975, 1982d), the Elmisauridae was established by Osmólska (1981), and consists of three taxa: *Chirostenotes pregracilis*, *Elmisaurus rarus*, and *Macrothalangia canadensis*. All three taxa may be synonymous and its recognition as a family was hesitantly retained as valid by Gauthier (1986). *Chirostenotes pregracilis* is from the Horseshoe Canyon Formation, Alberta (Gilmore, 1924a). *Elmisaurus rarus* is from the Nemegt For-

mation, Mongolian People's Republic. *Macrothalangia canadensis*, described by Sternberg (1932), is from the Horseshoe Canyon Formation, Alberta. Currie and Russell (Currie, pers. comm., 1985) believed that *Macrothalangia canadensis* is a junior synonym of *Chirostenotes pregracilis* and that the species *Caenagnathus collinsi* (see Caenagnathidae, above) may also be a junior synonym (Currie, pers. comm., 1986). The range of this family is middle Campanian to late Campanian-early Maastrichtian. Gauthier (1986) relegated the family Elmisauridae to the *Coelurosauria incertae sedis*.

"ENIGMOSAURIDAE." The monotypic family "Enigmosauridae" was recently established by Barsbold and Perle for the reception of the theropod species *Enigmosaurus mongoliensis* from the "Upper Chalks" (Cenomanian) of southeast Mongolia (Barsbold, 1983). This taxon is here considered to belong to the Theropoda and does not warrant familial recognition based on the characters given for the Theropoda as defined by Gauthier (1986).

"FABROSAURIDAE." The family "Fabrosauridae" includes six species that range from Late Triassic through Early Cretaceous time (Weishampel and Weishampel, 1983). Galton (pers. comm., 1985) reported that there are now two Late Cretaceous records of "fabrosaurids," both based on two undescribed isolated teeth, one from the Judith River Formation, Alberta, and the other from the Hell Creek Formation, Montana. Until these teeth have been demonstrably shown to be "fabrosaurids" based upon shared-derived characters and/or have not been reworked from older strata, I tentatively take the position that the youngest unquestionable "fabrosaurid" occurrence is Early Cretaceous. I therefore do not include this taxon in my chart (Table 1).

HADROSAURIDAE. Brett-Surman (1979) presented an analysis of the genera of the family Hadrosauridae based on features of the hadrosaurid pelvis. He recognized 21 valid genera that range from "pre"-Santonian through late Maastrichtian time. Only six genera recognized by him (*Edmontosaurus*, *Hypacrosaurus*, *Parasaurolophus*, *Saurolophus*, *Secernosaurus*, and *Shantungosaurus*) approach, or encounter, the Cretaceous-Tertiary boundary. Unfortunately, Brett-Surman (1979) did not give accurate stratigraphic ranges for most of the hadrosaurids. Weishampel and Weishampel (1983) offered a more complete account of Late Cretaceous hadrosaurs in their list of ornithopod taxa. They recognized 27 genera and 37 hadrosaur species occurring in Late Cretaceous units. Six of these 34 species have unquestionable ages. Only two species of *Edmontosaurus*, *E. regalis* and *E. edmontoni*, are considered valid, with all species previously assigned to "*Anatosaurus*" recognized as junior synonyms of *Edmontosaurus* with the exception of "*A. copei*," a species that represents a yet undescribed genus (Brett-Surman, 1979). *Edmontosaurus* is the only hadrosaurid to encounter the K-T boundary.

Parasaurolophus sp. has been reported from the North Horn Formation of Utah by Gilmore (1946) and Weishampel and Jensen (1979), and is considered here as being late Campanian to early Maastrichtian in age. Three species of *Parasaurolophus* have been described: *P. walkeri* from the Horse-

shoe Canyon Formation, *P. tubicen* from the "Ojo Alamo Sandstone" (=Naashoibito Member) of the Kirtland Shale, and *P. cyrtocrestatus* from the Fruitland Formation. These are all pre-middle Maastrichtian correlatives (see Table 2).

The hadrosaurid *Sauroplophus* is known by three species: *S. angustirostris* from the upper white beds of Khermeen Tsav, questionably from the beds of Bugeen Tsav, and from the Nemegt Formation, Mongolian People's Republic (Gradzinski et al., 1977; Maryńska and Osmólska, 1981c); *S. kryschtofovici* from "Upper Cretaceous" deposits of Amur, U.S.S.R., named on the basis of an ischium fragment (Rozhdestvensky, 1973), and undoubtedly a *nomen dubium*; and *S. osborni* from the Horseshoe Canyon Formation, Alberta (Brown, 1913). *Hypacrosaurus* is known by one species *H. altispinus* from both the Horseshoe Canyon Formation, Alberta, and the Two Medicine Formation, Montana. The primitive hadrosaur *Maiaasaura peeblesorum* is known from the Two Medicine Formation of western Montana (Horner and Makela, 1979; Horner, 1983).

The hadrosaurid *Secernosaurus koeneri* from the "Upper Cretaceous" of San Jorge Formation of Patagonia was diagrammed by Brett-Surman (1979) as late Maastrichtian in age, yet he did not document this stratigraphic correlation. *Secernosaurus koeneri* is known from a single (and much incomplete) specimen. *Barsboldia sicinski* is a lambeosaurine from the Nemegt Formation, Mongolian People's Republic (Maryńska and Osmólska, 1981c).

The Chinese hadrosaurid *Shantungosaurus giganteus* described by Hu (1973) is known from strata below an "Upper Cretaceous" sequence (Wangshih series) and is questionably Maastrichtian as are *Taninus chingkankouensis*, *T. sinensis*, and *Tsintaosaurus spinorhinus*.

Other hadrosaurs recognized as valid taxa include: *Araucosaurus tuberiferus*, from the Beletinskaya Formation (Turonian-Santonian) of Kazakhstan (U.S.S.R.); *Bactrosaurus johnsoni* and *Gilmoresaurus* (=Mandschuosaurus) *gilmorei*, from the Iren Dabasu (=Iren Nor) Formation (Cenomanian), People's Republic of China; *Brachylophosaurus canadensis*, from the Oldman Formation, Alberta; *Claosaurus agilis*, from the Niobrara Chalk, Kansas; *Corythosaurus casuarius*, from the Oldman Formation, Alberta; *Hadrosaurus foulkii*, from the Marshalltown, Merchantville, and Woodbury formations, New Jersey; *H. navajovius*, from the Fruitland and Kirtland formations, New Mexico; *H. notabilis*, from the Oldman Formation, Alberta and the Bear Paw Shale, Western Interior; *Jaxartosaurus arelensis*, from Coniacian-Santonian strata of Kazakhstan (U.S.S.R.); *Lambeosaurus lambei* and *L. magnicristatus*, both from the Oldman Formation, Alberta; the questionable ?*Lambeosaurus laticaudus*, from the "El Gallo Formation," Baja California; *Lophorhotos atopus*, from the Black Creek Formation, North Carolina; *Nipponosaurus sachalinensis*, from Coniacian-Santonian strata of Japan; *Orthomerus dolli*, from the Maastricht beds of the Netherlands; "*Procheneosaurus*" *convincens*, from the Dabrazinskaya Formation (Santonian) of the U.S.S.R.; and lastly *Prosauroplophus maximus*, from the Oldman Formation, Alberta (Brett-Surman, 1979; Weishampel and Weishampel, 1983; Weishampel and Horner, 1986). Of the aforementioned hadrosaurids, only two species are known

with certainty from late Maastrichtian strata and six others are known from pre-late Maastrichtian deposits. The majority of hadrosaurid species are known from Campanian strata. Clearly hadrosaurid diversity reached its zenith in middle Campanian times and hadrosaurid species were severely diminished by the late Maastrichtian.

"**HYPSILOPHODONTIDAE.**" The family "Hypsilophodontidae" is a polyphyletic family (Gauthier, 1986), which is represented by only two or three species in the Late Cretaceous. These Late Cretaceous "hypsilophodontids" include: *Parksosaurus warreni* from the Horseshoe Canyon Formation, Alberta, and *Kangnasaurus coetzeei* from the Maastrichtian Kalahari deposits of South Africa. The taxon *Thescelosaurus neglectus*, which has been included in this polyphyletic group by Galton (1974), is treated separately below. Galton (1974) cited "*Laosaurus*" *minimus* from the Late Cretaceous; however, this taxon is from Early Cretaceous strata (Gilmore, 1924b). The above taxa are the last survivors of a polyphyletic family that includes some 16 species spanning Callovian (early Late Jurassic) to late Maastrichtian time and whose maximum species diversity was reached during the Late Jurassic and Early Cretaceous. Galton (pers. comm., 1985) reports that he is presently describing a new genus from the Hell Creek Formation of South Dakota previously referred to *Thescelosaurus*.

"**IGUANODONTIDAE.**" Out of the 19 species that are currently recognized as being members of this polyphyletic family, only three species are known from late Senonian strata. The oldest of these, *Craspedon lonzeensis*, is from the Santonian or Belgium; *Radinosaurus alcinus* is from the Gosau Formation (Campanian) of Austria; and *Mochlodon suessi* is from both the Gosau Formation (Campanian) of Austria and the "Danian" beds (which are pre-late Maastrichtian) of Romania (Weishampel and Weishampel, 1983). As with the preceding family "Hypsilophodontidae," the "Iguanodontidae" reached its maximum species diversity (Late Jurassic-Early Cretaceous) well before the outset of the Maastrichtian.

"**MEGALOSAURIDAE.**" The family "Megalosauridae" includes a number of pre-late Maastrichtian (mostly middle Late Jurassic) taxa, too numerous to cite here. The family is not recognized here and is included within the Carnosauria as defined by Gauthier (1986). A number of taxa included in this family are based on very incomplete material.

NODOSAURIDAE. Six major nodosaurid genera (*Hylaeosaurus*, *Nodosaurus*, *Panoplosaurus*, *Sauropelta*, *Silvisaurus*, and *Struthiosaurus*) are currently recognized (Coombs, 1978). Three genera previously included within this family have been transferred to the family Ankylosauridae (Coombs, 1978, see above). The last occurrence of the nodosaurids is in strata of early to middle Maastrichtian age and includes the species *Struthiosaurus transilvanicus*, *Panoplosaurus mirus*, *P. rugosidens* (=Edmontonia *rugosidens*, =Palaeosincus *rugosidens*) and *P. longiceps* (Coombs, 1978). "*Edmontonia*" sp., which may, in part, be distinct from *Panoplosaurus*, has been recently reported in the lower Lance, Hell Creek, and Laramie formations of North America and is inferred to have undergone significant reduction in frequency of individuals by this time (Carpenter and Breithaupt, 1986).

ORNITHOMIMIDAE. Gauthier (1986) recognized 12

species in this family, which was revised to include not only the Ornithomimidae of Marsh (1890) but also the "Deinocheiridae" of Osmólska and Roniewicz (1970). Russell (1972) redefined the family and provided stratigraphic data for many of the species. The taxa recognized by Gauthier as belonging to this family include: *Archaeornithomimus asiaticus* from the Cenomanian Iren Dabasu Formation, People's Republic of China; *Deinocheirus nirificus* from the Nemegt Formation, Mongolian People's Republic; *Dromiceiomimus brevitertius* from the Horseshoe Canyon Formation, Alberta; *D. samueli* from the Oldman Formation, Alberta; *Elaphtrosaurus bambergi* from Late Jurassic strata, Tanzania, East Africa; *Gallimimus bullatus* from the Nemegt Formation, Mongolian People's Republic; *Garudimimus brevipes* from "early Senonian" strata, of southeast Mongolia; *Ingenia yanshini* from "late Senonian" strata, southeast Mongolia; *Ornithomimus edmonticus* from the Oldman and Horseshoe formations, Alberta; *O. sedens* from the Lance Formation, Wyoming (perhaps a junior synonym of *O. velox*); *O. velox* from the Denver Formation, Colorado; and *Struthiomimus altus* from the Oldman Formation, Alberta. *Avimimus portentosus* is now known to be a "bird" (Gauthier, pers. comm., 1985). Russell (1972) reported indeterminate ornithomimids from latest Cretaceous (Lance equivalent) strata in addition to the type "*Ornithomimus velox*" from the Denver Formation, Colorado. More recently, DeCourten and Russell (1985) reported this species from the Kaiparowits Formation of southern Utah and suggested a late Maastrichtian age for this formation on the basis of palynomorphs reported by Lohrengel (1969). However, the palynomorphs reported by Bowers (1972) and the occurrence of *Parasaurolophus* are consistent with a late Campanian–early Maastrichtian age for this sequence. Furthermore, the possibility of *Ornithomimus velox* in strata older than late Maastrichtian cannot be ruled out. Eaton (pers. comm., 1986) believes the evidence in either case is not conclusive, and that recent data support a pre-late Maastrichtian age for this unit.

PACHYCEPHALOSAURIDAE (includes "Homalocephalidae"). Twelve monotypic genera comprise the bizarre ornithopod family Pachycephalosauridae: *Goyocephale latimorei* from the Boro Khouil beds, People's Republic of Mongolia; *Gravitholus albertae* from the Oldman Formation, Alberta; *Heishanosaurus pachycephalus* from the Chia-yü-kuan "formation," People's Republic of China; *Micropachycephalosaurus hongtuyanensis* from the Wong Formation (Campanian) of Laiyang, Shantung, People's Republic of China; *Mujungatholus atops* from the Grès de Maevarano (Campanian) of Madagascar (Sues and Taquet, 1979); and *Homalocephale calathoceros* and *Prenocephale prenes*, both from the Nemegt Formation, People's Republic of Mongolia. *Pachycephalosaurus* includes only one species, *P. wyomingensis*. "*P. reibeimeri*" and *P. wyomingensis* were previously considered probable junior synonyms and females of "*P. grangeri*" (Galton, 1971) and all are known from the Lance Formation, Montana, South Dakota, and Wyoming, respectively. However, a recent reassessment by Galton and Sues (1983) suggests that *P. wyomingensis* is probably a sub-adult male and that all species of *Pachycephalosaurus* are referable to *P. wyomingensis*. Six species of *Stegoceras* have

been named: *S. bexelli* ("Upper Cretaceous" of Tsondolein = Khuduk, northwest Mongolia); *S. browni* from the Oldman Formation, Alberta; *S. edmontonicus* from the Horseshoe Canyon Formation, Alberta; *S. lambei* from the Oldman Formation, Alberta; and *S. sternbergi* and *S. validus*, both from the Horseshoe Canyon Formation, Alberta. *Stegoceras lambei* and *S. sternbergi* are probably junior synonyms of *S. validus*, which includes *S. brevis* (Galton, 1971). The taxon *Ornatolithus* was recently established for "*S.*" *browni* (Galton and Sues, 1983). *Stygimoloch spinifer*, a taxon based on a massive, but fragmentary spiny horn core fused to a squamosal, is from the Lance (Hell Creek) Formation, Montana (Galton and Sues, 1983) and is probably a *nomen dubium*. *Tyrocephale gilmorei* is from the Barun Goyot Formation, People's Republic of Mongolia; *Wannosaurus yansiensis* is from the Xiaoyan Formation, Anhui Province, People's Republic of China, and is of indeterminate Late Cretaceous age. The oldest certain occurrence of the family Pachycephalosauridae is middle Campanian. If the taxon *Yaverlandia bitholus* from the Early Cretaceous Wealdon beds of England proves to be in fact a primitive pachycephalosaurid, then the range of this family covers most of Cretaceous time. The majority of the pachycephalosaurid taxa are known from pre-late Maastrichtian strata indicating that species diversity was significantly reduced by late Maastrichtian time (Bohlin, 1953; Galton, 1971; Maryńska and Osmólska, 1974; Gradziński et al., 1977; Lian-hai, 1977; Dong, 1978; Sues and Taquet, 1979; Wall and Galton, 1979; Sues, 1980; Perle et al., 1982; and Galton and Sues, 1983).

***Pachyrhinosaurus canadensis*.** The "Pachyrhinosauridae" was established by Sternberg (1950) for the monotypic taxon *Pachyrhinosaurus canadensis* from the Horseshoe Canyon Formation, Alberta. Langston (1967) believed that this species should be included within the family Ceratopsidae (above), but Charig (1979) considers a separate family to be warranted. However, because monotypic families are viewed as redundant, only the species is recognized. *Pachyrhinosaurus canadensis* is probably a true ceratopsid, but for argument's sake it is treated separately here. *Pachyrhinosaurus canadensis* is restricted to the middle Campanian.

PROTOCERATOPSIDAE. Five genera representing some six species constitute the taxa included in the family Protoceratopsidae. *Bagaceratops rozhdestvenskyi* is from the middle Campanian red beds of Khermeen Tsav I and II, Mongolian People's Republic (Gradziński et al., 1977; Maryńska and Osmólska, 1981b). *Leptoceratops gracilis* is from the Horseshoe Canyon Formation, Alberta. Although Fox (1978) cited this dinosaur from the "Lance Formation," Ostrom (1978) correctly pointed out the improper use of the "Lance" beds and demonstrated that *Leptoceratops gracilis* is from a horizon that is correlative to the Horseshoe Canyon Formation (late Campanian–early Maastrichtian). *Microceratops* is represented by two species *M. gobiensis* and *M. sulcidens* (the latter species is known only by very incomplete material and is probably a *nomen dubium*). Both species are from the "Late Cretaceous" (pre-late Maastrichtian) deposits of China. *Montanaceratops* is known by the sole species *M. cerorhynchus* from the St. Mary River Formation, Montana. *Protoceratops andrewsi* is the well-known species from the

Djadokhta Formation, Mongolian People's Republic, and the "Upper Cretaceous" of Ulan, northwest China (Steel, 1969). The species *Protoceratops kozlowskii* is from the middle Campanian Barun Goyot Formation, Mongolian People's Republic (Maryńska and Osmólska, 1981b). The family Protoceratopsidae ranges from the middle Campanian to early Maastrichtian.

SAUROPODOMORPHA/TITANOSAURIDAE. Numerous sauropodomorph families have been said to occur in Late Cretaceous units worldwide. These families include the Brachiosauridae (for the occurrence of *Rebbachisaurus garasbe* from Cenomanian deposits of Niger [Lavocat, 1954]); the ?Cetiosauridae (for the occurrence of *Quaesitosaurus orientalis* from the middle Campanian of Mongolian People's Republic [Kurzhanov and Bannikov, 1983]); and the Caramasauridae (for the occurrence of *Opisthocoelecaudia skarzynskii*, Borsuk-Białynicka, 1977) and Diplodocidae (for the occurrence of *Nemegtosaurus mongoliensis*, Nowsinski, 1971), both from the Nemegt Formation, Mongolian People's Republic. Various taxa have been attributed to the family Titanosauridae, including "*Laplatasaurus*" *madagascariensis* (Campanian) of Madagascar (D. Russell et al., 1976), *Titanosaurus indicus*, *Antarctosaurus septentrionalis* (?Maastrichtian), and many others. The abundance of sauropodomorph taxa named is directly proportional to the very fragmentary remains upon which many of the species have been based. My comments here for the Titanosauridae apply to the Late Cretaceous sauropodomorphs in general. Given the nature of the fossil record of these taxa an accurate species assessment of sauropodomorph taxa is not possible at this time.

Some of the more important Late Cretaceous sauropodomorphs include: *Alamosaurus sanjuanensis*, a form genus from the late Campanian-early Maastrichtian North Horn and Kirtland formations of Utah and New Mexico, respectively, which has been reported from the Javelina Formation (?late Maastrichtian) of Texas (see Mateer, 1981 for a discussion of the dubious nature of this taxon which is believed to be the latest titanosaurid); *Antarctosaurus giganteus* from the "Senonian" of Aquada del Cano (Neuquén), Argentina; *A. septentrionalis* (which includes the type species *Titanosaurus indicus*) from the Lameta beds ("Late Cretaceous" see Chatterjee, 1978) of Madhya Pradesh, India; and *A. wichmannianus* from the "Senonian" of both Argentina and Uruguay (Steel, 1970). It is unclear whether all "*Titanosaurus*" species are referable to *Antarctosaurus*. However, "*Titanosaurus*" has priority as the genus name. Numerous species of "*Titanosaurus*" have been proposed and they are not all valid for reasons given above.

Other Late Cretaceous sauropodomorph taxa include: *Aegyptosaurus baharijensis* from the Baharije Formation (early Campanian) of northern Egypt; *Argyrosaurus superbus*, from the Arenscio Formation (Senonian) of Argentina and Uruguay (Bonaparte, 1978); *Camphylodoniscus ameghinoi* from Campanian strata of Argentina; *Chianyuosaurus* (= *Euheleopus*) *lacustris* from the "Late Cretaceous" Chia-yü-kuan "formation," People's Republic of China (Bohlin, 1953); *Chubutisaurus* from the Campanian of Argentina (Bonaparte and de Gasparini, 1979); *Hypselosaurus priscus* from the

"Begudo-Rognacian beds" (Maastrichtian) of France (Jeletsky, 1960, 1962); the questionable sauropod *Hypsibema missouriensis* from the Ripley Formation (early Maastrichtian) of Missouri and *H. crassicauda* (a possible hadrosaur, see Baird and Horner, 1982); *Laplatasaurus araukanicus* from the Neuquén Group (Senonian) of Argentina (Bonaparte, 1978; Bonaparte and Powell, 1980); "*L.*" *madagascariensis* from Campanian strata of both Madagascar and India; *Loricosaurus scutatus* (a possible ankylosaurian) and *Microcoelus patagonicus* both from the Neuquén Group (Senonian) of Argentina (Bonaparte, 1978; Bonaparte and Powell, 1980); *Nemegtosaurus mongoliensis* from the Djadokhta Formation, Mongolian People's Republic (Nowinski, 1971); *N. pachi* from the Subash Formation, Turfan, Xinjiang, People's Republic of China (Dong, 1977); *Salatasaurus loricatus* (= *Titanosaurus australis*) from the Lecho Formation (late Campanian-early middle Maastrichtian) of Argentina (Bonaparte and Powell, 1980); *Sphaeroror erbeni* from "Upper Cretaceous" strata of Uruguay (Mones, 1980); and the poorly known *Succinodon putzeri* based on teeth from Campanian age strata of Poland (Huene, 1941). On the face of it, it appears as though there was great diversity in sauropodomorph taxa during the Late Cretaceous. However, it is certain that many of these taxa are not valid, having been named on very incomplete and otherwise undiagnostic material as previously mentioned. In addition, most if not all of these taxa come from units that are of pre-late Maastrichtian age.

"SAURORNITHOIDIDAE." Barsbold (1974) established this family for the taxon *Saurornithoides* which is a junior synonym of *Troodon* (see Troodontidae, below).

SEGNOSAURIDAE. Two species comprise the family Segnosauridae (Perle, 1979) which includes *Erlikosaurus andrewsi* and *Segnosaurus galbinensis* both from the Bayn Shireh "formation," Baysheer Tsav, Mongolian People's Republic (Barsbold and Perle, 1980). A problematic taxon *Nanshiungosaurus brevispinus* from the Nanxiong Formation, People's Republic of China, may also belong to this family, but at present is too poorly known to definitively assign to the Segnosauridae. This family includes taxa from pre-late Maastrichtian deposits and became extinct by middle Santonian time. Segnosaurids are viewed as being transitional between "prosauropods" and ornithischians (Paul, 1984b).

"SHANSHANOSAURIDAE." This monotypic family established for the taxon *Shanshanosaurus huoyanshanensis* from the Subash Formation, Xinjiang, Turfan Basin, China (Dong, 1977) is not recognized here as valid and is relegated to *Theropoda incertae sedis*.

"SPINOSAURIDAE." This family includes five valid species which are included here in the Carnosauria following Gauthier (1986). The youngest species is *Spinosaurus aegypticus* from the early Cenomanian Baharije Formation of Egypt. A newly discovered thoracic vertebra, bearing an enlarged neural spine, from the Naashoibito Member of the Kirtland Shale, suggests the presence of either the carnosaur *Spinosaurus* or the hadrosaur *Ouranosaurus*. This specimen is currently being studied and its taxonomic identity, at present, remains uncertain (Dobie, pers. comm., 1985).

"THERIZINOSAURIDAE." The monotypic family

“Therizinosauridae” was established for the carnosaurian-like taxon *Therizinosaur cheloniformes* (Maleev, 1954; Barsbold, 1976). Although this taxon was not discussed by Gauthier (1986) it is best to consider this species within the Carnosauria without formal familial designation. *Therizinosaur cheloniformes* is from the Nemegt Formation and the “upper white beds” of Khormeen Tsav, Mongolian People’s Republic (Gradziński et al., 1977). This taxon is restricted to the middle Campanian.

***Thescelosaurus neglectus*.** The family “Thescelosauridae” was established by Sternberg (1937) for the species *Thescelosaurus neglectus*. The species *T. edmontonensis* was named by Sternberg (1940) and was later considered a probable junior synonym of *T. neglectus* by Galton (1974), a view that is accepted here. *Thescelosaurus neglectus* is known from the Horseshoe Canyon, Lance Creek, Frenchman, Scollard, and Hell Creek formations of North America (Galton, 1974). Galton (1974) also reviewed the systematic position of *Thescelosaurus* in the ornithomimid families (“Hypsilophodontidae,” “Camptosauridae,” and “Iguanodontidae”) and concluded that *Thescelosaurus* was a generalized (“conservative”) ornithomimid belonging to the family “Iguanodontidae.” It is recognized here as a taxon independent of family ranking.

“TROODONTIDAE.” This family, which takes its name from the species *Troodon formosus* (Leidy, 1856) has recently been demonstrated to be the senior synonym of *Stenonychosaurus inequalis* and *Pectinodon bakkeri* (Currie, 1987). In his review of the “Saurornithoididae,” Carpenter (1982) synonymized *Stenonychosaurus inequalis*, *Ornithomimus* (in part), and *Polyodontosaurus grandis* (along with *Troodon formosus* and the “Saurornithoididae”) as junior synonyms of *Saurornithoides*, failing to recognize seniority of *Troodon* and earlier synonymies (see Currie, 1987, for full discussion). The family Troodontidae tentatively includes three species: *Saurornithoides junior* from the Nemegt Formation, Mongolian People’s Republic; *S. mongoliensis* from the Djadokhta Formation, Mongolian Peoples’ Republic (which may be a junior synonym of *S. junior*, see Gauthier, 1986:11); and *Troodon formosus* from the Horseshoe Canyon, Lance, and Hell Creek formations (Carpenter, 1982; Currie, 1987). The family Troodontidae ranged from the middle Campanian to late Maastrichtian.

DINOSAURIA incertae sedis. There are a few species of Late Cretaceous dinosaurs that may or may not be valid, and that clearly do not fall within currently recognized families owing to their fragmentary nature and/or poorly understood phylogenetic relationships. Some of these dinosaur species include: *Aublysodon mirandus*, a problematic theropod known only by teeth from the middle Campanian to late Maastrichtian of North America (Carpenter, 1982); *Hulsanapes perlei* from the Barun Goyot Formation, Mongolian People’s Republic (Osmólska, 1982) which is included within the Coelurosauria incertae sedis by Gauthier (1986); the ?coelurosaur *Noasaurus leali* from the Lecho Formation (late Campanian or early Maastrichtian) of northwestern Argentina (Bonaparte and Powell, 1980); the “tooth taxon” *Paronychodon lacustris* from the late Maastrichtian Lance Formation, which may be valid, and possibly belongs to either the Dromaeosauridae or Troodontidae (=Saurornithoididae

Table 3. List of probable valid “dinosaurian” taxa (paraphyletic sense, exclusive of the Avialae, Figure 1) for the latest Cretaceous (late Maastrichtian).

Taxon	Source
<i>Albertosaurus lancensis</i>	Russell, 1970
<i>Ankylosaurus magniventris</i>	Coombs, 1978
<i>Avisaurus archibaldi</i>	Brett-Surman and Paul, 1986
<i>Edmontosaurus edmontoni</i>	Brett-Surman, 1979
<i>E. regalis</i>	Brett-Surman, 1979
“ <i>Edmontonia</i> ” sp. (or <i>Panoplosaurus</i>)	Carpenter and Breithaupt, 1986
Ornithomimidae indet.	Russell, 1972
<i>Pachycephalosaurus wyomingensis</i>	Galton, 1971; Galton and Sues, 1983
<i>Thescelosaurus neglectus</i>	Galton, 1974
<i>Torosaurus latus</i>	Steel, 1969
<i>Triceratops horridus</i>	Ostrom and Wellnhofer, 1986
<i>Tyrannosaurus rex</i>	Gauthier, 1986

of Carpenter, 1982) (Currie, 1987); and *Saurornitholestes langstoni* from the Judith River Formation, Alberta (Sues, 1978), a taxon placed within the Coelurosauria incertae sedis by Gauthier (1986). A few of these taxa are known from late Maastrichtian strata, but because of their uncertain nature, they do not substantially affect the number of species that existed at the time of the K–T transition (see Table 3).

PTEROSAURIA

AZHDARCHIDAE. Padian (1984) recognized two Late Cretaceous pterosaur families, the Pteranodontidae (Albian–Campanian, see below) and the family “Titanopterygiidae” (Campanian–Maastrichtian). This latter family, which was replaced by the family Azhdarchidae (Padian, 1986) because of taxonomic priority, is based on characters of the cervical vertebrae and includes only three taxa, *Azhdarcho lanciollis* (Nesov, 1984), *Quetzacoatlus northropi*, and *Titanopteryx philadelphiae*, which in fact may be coeval (Padian, 1984, 1986). The Azhdarchidae ranged from the middle Campanian to late Maastrichtian.

PTERANODONTIDAE. The pterosaurs, by all indications, were severely diminished in number of taxa by the beginning of the Maastrichtian. Russell (1975, 1982d) illustrated in his diagrams the pterosaur family Ornithocheiridae extending to the K–T boundary. Wellnhofer (1978) indicated that the family Ornithocheiridae ranged from the Cenomanian through Turonian (early–Late Cretaceous) with all species becoming extinct well before the end of the Cretaceous. No other pterosaur families were cited by Russell (1975) for the Late Cretaceous. In his subsequent paper (Russell, 1982d), his diagram had been modified to include an “unnamed family” of pterosaurs for which he provided no additional information. Recently Padian (1984) diagnosed the pterosaur family Pteranodontidae based on the presence of a distinct deltopectoral crest. Taxa recognized as belonging to this family included: *Nyctosaurus gracilis*, *N. bonneri*, *Pteranodon in-*

gens, *P. longiceps*, *P. marshi*, *P. occidentalis*, *P. sternbergi*, and *P. walkeri*. All of these taxa are known from the upper part of the Niobrara Formation, which is early Campanian in age. The taxa "*Ornithostoma*" (= *Pteranodon*) *orientalis* from Serdowa, Saratow District, Petrowsk, U.S.S.R., and *Dyctosaurus lamegoi* from the Gramame Formation of Brazil are probably pre-late Maastrichtian in age (Wellnhofer, 1978). If the above species are valid, maximum species diversity for the family Pteranodontidae was reached at the time of their extinction, near middle Campanian time.

ICHTHYOSAURIA

PLATYPTERYGIIDAE. The greatest taxonomic diversity of ichthyosaurs occurred during the Jurassic, well before the close of the Cretaceous. Russell (1975, 1982d) illustrated the range of the ichthyosaur family Platypterygiidae as extending to late Campanian time. The unusually late range extension for this family is based on an isolated occurrence of a single coracoid from a supposed late Campanian ichthyosaur reported by McGowan (1973). Regardless of whether this specimen was reworked or not, ichthyosaurs are not known from any Upper Cretaceous deposits of late Maastrichtian age and the major reduction of ichthyosaur taxa occurred well before Cenomanian time (Russell, 1975). Russell (1982d), as with the preceding Pterosauria, diagrammed an "unnamed family" without documentation.

SUMMARY AND CONCLUSIONS

The foregoing review of K-T transitional reptiles and their biostratigraphic distribution allows for a reassessment of these taxa with respect to the Cretaceous-Tertiary boundary and enables one to comment on the supposed mass extinction of these vertebrates at the close of the Cretaceous Period.

In general, the turtles are known by numerous species, many of which cross the Cretaceous-Tertiary boundary (Hutchison and Archibald, 1984, 1986). Despite the fact that most turtle groups are probably over-split in terms of numbers of species (and genera), the chelonians still appear to be relatively diverse at the species level. Unfortunately, at this time precise numbers of turtle taxa that encounter the K-T boundary on a global scale cannot be assessed, but work by Hutchison and Archibald (1984, 1986) and others will undoubtedly help to resolve turtle species diversity at the K-T boundary. Based on the available evidence, both marine and freshwater turtles were little affected by the K-T transition.

The eosuchian *Champsosaurus laramiensis* is known from both sides of the K-T boundary indicating that this taxon was unaffected by the K-T transition.

In North America, the lizard species *Odaxosaurus piger*, *Contogenys sloani*, *Palaeosaniwa canadensis*, and *Exostinus lancensis* are known from strata on both sides of the K-T boundary. Lizards for the most part are best documented in Cenozoic strata. Numerous lizard families are known from species that diversified in Tertiary time, many in the early Paleogene. Terrestrial lizard diversity was not affected by the K-T transition, with the exception of changes in geographic

PLESIOSAURIA

ELASMOSAURIDAE. The biostratigraphic data for plesiosaurs presented by Russell (1975) were largely misrepresented. Only one plesiosaur family (Elmosauridae) is known from the Late Cretaceous. The families Cimoliasauridae and Polycotylidae listed by Russell (1975, 1982d) are not recognized as valid owing to the numerous species contained within these two families that are recognized as *nomina dubia* and others that have been synonymized (Welles, 1962). None of the plesiosaur species that Russell discussed are known from late Maastrichtian marine deposits (Welles, 1943, 1949, 1952, 1962). The youngest documented occurrence of plesiosaurs (and ?pliosaurus) include the following taxa: *Aphrosaurus furlongi*, *Fresnosaurus dredcheri*, *Hydrotherosaurus alexandrae*, and *Morenosaurus stocki*, all from the Moreno Formation of California, which is considered pre-late Maastrichtian (Popenoe et al., 1960); ?*Aristonectes parvidens* (a probable pliosaur from the Cañadon del Loro strata, Patagonia) (Welles, 1962); *Lewrospodylus ultimus* (from the Horseshoe Canyon Formation of Alberta); and *Mauisaurus haasati* (a "composite" plesiosaur from many localities in New Zealand) (Welles, 1962). Suffice it to say that, like the ichthyosaurs, the plesiosaurs experienced maximum species diversity prior to the onset of the Maastrichtian and that they were most abundant in Late Jurassic time.

distribution for some groups, such as the teiids. The aquatic lizards, mosasaurs, reached their zenith in terms of species diversity, prior to the late Maastrichtian and no representatives of this once diverse group are known with certainty from late Maastrichtian marine rocks. Amphisbaenians are not known from the Late Cretaceous and are still a very rare component of reptilian species known.

Crocodylians from the Late Cretaceous and early Paleogene have not been studied in the detail necessary to assess accurately the precise number of species that cross the Cretaceous-Tertiary boundary. However, the genus *Leidyosuchus* is known from both sides of the K-T boundary and it is clear that crocodylians in general were certainly an abundant part of the reptilian component for both the Late Cretaceous and early Paleogene herpetofaunas and were well established on both sides of the K-T boundary. It is doubtful that crocodylian species diversity differed significantly in post-Cretaceous time, a fact that is commonly pointed out by paleontologists citing the crocodylians as one of the true success stories of the K-T transition.

The most controversial taxa, in terms of their "conspicuous absence" in post-Cretaceous strata, are of course the "dinosaurs" (traditional or paraphyletic sense). As I have outlined above, many of the recognized primitive dinosaurs experienced major declines in diversity of species well before late Maastrichtian times. These include the Ankylosauridae, Caenagnathidae, the taxon Carnosauria (including the family Tyrannosauridae), Ceratopsidae, Dromaeosauridae, Elmi-

sauroidea, Hadrosauridae, "Hypsilophodontidae," "Iguanodontidae," Nodosauridae, Ornithomimidae, Pachycephalosauridae, Pachyrhinosauridae, Protoceratopsidae, the taxon Sauropodomorpha (including the family Titanosauridae), and the Segnosauridae. All of these groups either became extinct or were severely reduced in number of species, without exception, before the late Maastrichtian. A few groups include three or fewer taxa (Caenagnathidae, Elmsauridae, Troodontidae, and Segnosauridae) and thus in themselves are not diverse. Contrary to the arguments of Russell (1975, 1979, 1982b, 1982d) based principally on numbers of specimens rather than species, "dinosaur" species were more diverse earlier in the Late Cretaceous and are represented by few species in late Maastrichtian strata (Ankylosauridae, Dromaeosauridae, Hadrosauridae, "Hypsilophodontidae," Ornithomimidae, Pachycephalosauridae, and the Carnosauria) which argues vigorously against the concept of a mass extinction of dinosaurs at the end of the Cretaceous Period. Only 12 to 14 species of dinosaurs (paraphyletic sense) are considered to be of late Maastrichtian age (Table 3).

The pterosaurs clearly had their heyday prior to the close of the Cretaceous Period, having reached their maximum species diversity in Late Jurassic to early Late Cretaceous (Campanian) times. Ichthyosaurs and plesiosaurs also experienced maximum species diversity and extinction before the end of the Late Cretaceous. All these three groups clearly experienced dwindling numbers of species in response to their shrinking habitat, the draining shallow epicontinental seas of the Late Cretaceous.

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Thus, there is no overwhelming evidence to support an isochronous mass extinction of dinosaurs, marine, flying or other terrestrial reptiles at the close of the Cretaceous. Catastrophic mass extinction theories are flawed because they cannot account for the selectivity of the extinction of dinosaurs and these theories fail to recognize basic phylogenetic relationships. The apparent reduction of primitive dinosaurian taxa at the end of the Cretaceous Period appears to have coincided with the radiation of the more advanced dinosaurs (birds), during this time in geologic history. Because Aves is included as a clade within the Dinosauria (Bakker and Galton, 1974; Bakker, 1975; Cracraft, 1986; Gauthier, 1986), the apparent radiation of Aves concurrent with the decline of primitive dinosaurian taxa (as suggested by the waning stage of Zhao, 1983), is an interesting point of fact. Evidence for major avian speciation in the Late Mesozoic has been given recently by Sibley and Ahlquist (1986) and the group's proliferation during the Cenozoic demonstrates that these dinosaurs are as successful as their Mesozoic counterparts. Restriction of the term "dinosaur" to include only those taxa represented by the more archaic Mesozoic forms, exclusive of the birds, results in a group that is unnatural, which it is not. Cracraft (1986:384) succinctly stated that "... if one excludes avian groups, the taxon Theropoda itself is an unnatural (paraphyletic) group..." This fact alone argues against a major isochronous catastrophic mass extinction of dinosaurs.

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